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Sexual Selection Revisited – Towards a Gender-Neutral Theory and Practice

A Response to Vandermassen's 'Sexual Selection: A Tale of Male Bias and Feminist Denial'

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ABSTRACT In a recent issue of this journal, Vandermassen suggested that feminists should include sexual selection theory and evolutionary psychology in a unifying theory of human nature. In response, this article aims to offer some insight into the development of sexual selection theory, to caution against Vandermassen's unre-served assimilation and to promote the opposite ongoing integration – an inclusion of gender perspectives into evolutionary biology. In society today, opinions about maintaining traditional sex roles are often put forward on the basis of what is natural and how animals behave. However, the natural sciences have proved to be pervaded by gendered values and interests; Darwin's theory of sexual selection has been criticized for being male biased, and partly due to the unwillingness of Darwin's scientific contemporaries to accept female choice, research has been overwhelmingly focused on males. More recently, theory has become less gender biased and research has come to include a large variety of issues not present in the first version of the theory. However, there is a need to increase the awareness of gender bias in order to develop a gender-neutral evolutionary biology.

KEY WORDS androcentric bias ♦ evolutionary biology ♦ evolutionary psychology ♦ history of science ♦ sexual selection

INTRODUCTION

In 2004, Griet Vandermassen presented an account of male bias in sexual selection theory in this journal and concluded by arguing for the assimilation

of evolutionary psychology into feminist theory (Vandermassen, 2004). As an evolutionary biologist, I oppose the simplified account of a unified sexual selection theory and I disagree with her conclusions for feminist theory. Therefore, my aims in this article are to give a brief overview of the androcentric bias present in sexual selection theory, provide an insight into contemporary theory and research, caution against Vandermassen's inclusion of evolutionary psychology into feminist theory, and finally, promote the integration of gender perspectives into evolutionary biology.

In the current debate about the relative importance of biology and culture for the formation of sex and sexuality, traditional opinions about sex roles and sexuality are often advocated based on claims of nature's order. However, gender analyses have shown how the natural sciences' supposedly objective and value-neutral facts about nature's order are pervaded by gendered values and interests (Harding, 2005). Feminist biologists have demonstrated the male bias present in biological theory and practice.¹

Theories of scientific progress suggest that development in modern science is dependent on the social context from which scientific innovations cannot be isolated. Science philosopher Donna Haraway (1989) has studied the development of primatology and her findings corroborate this view. According to her research, interpretations of primate behaviour mirror ideological change in the surrounding society. Primatology has not only been under the influence of current political ideologies, but has also been the means by which these ideologies have defined what is natural and morally acceptable (Haraway, 1989). A further example of the influence of current ideologies on behavioural ecology is the extensive overview of research on animal sexual behaviours done by Bruce Bagemihl (1999). He shows that adherence to Darwinian theory has blinded researchers to common homosexual behaviours in animals. He also suggests that variation in animals' sexual practices has often been suppressed due to the researchers' fear of being pointed out as homosexual. In more recent publications, variation in sexual behaviours has been reported, but these behaviours have still been interpreted in an ideological framework of human morals (Bagemihl, 1999). There is good reason to believe that presuppositions in animal behaviour research are still biased by society's ideological values.

SEXUAL SELECTION THEORY AND ITS ANDROCENTRIC BIAS

Here I present a survey of sexual selection theory and its criticisms with emphasis on what has made evolutionary biology gender biased.² Darwin's theory of natural selection is well supported by data and can largely explain the diversity of extant and extinct biological life. Natural

selection explains adaptive evolution as a result of enhanced survival of individuals possessing heritable traits in a certain environment, leading to higher frequency of those traits in following generations. In contrast, his theory on sexual selection has been widely debated. Sexual selection was aimed at explaining the occurrence of elaborate male traits that were obviously costly in terms of survival and therefore impossible to explain by natural selection. Sexual selection is a subset of natural selection in which the process is differential reproduction as opposed to differential survival. Darwin proposed two mechanisms by which sexual selection occurred: intersexual selection (between-sex interactions), mainly via female mate choice, and intrasexual selection (within-sex interactions), largely through contests between males. It is important to note that both these processes are examples of how variance in male reproductive success is generated, which is one reason why sexual selection in females has been considered less important.

Even though Darwin clearly thought that female choice was important, contemporary scientists did not recognize its significance partly because females were assumed to be passive in the mating process and partly because, for example, insects were not supposed to have the intellectual abilities to distinguish small aesthetic differences that were needed to perform a choice. This misapprehension has resulted in a massive skew towards a focus on males in sexual selection research. In behavioural ecology, e.g. the study of ecological and evolutionary basis for animal behaviour, the vast majority of both theoretical and empirical research has focused on male behaviour while leaving females mostly unstudied. It was not until the 1970s, when parental investment theory legitimated the study of female choice concurrently with many women scientists entering the field of primatology, that females began to be perceived as active subjects influencing evolutionary processes. This change in approach opened up the study of active female strategies. As one of many examples, in Hanuman langurs, the according-to-theory coy females were found to solicit sex from several males in order to confuse paternity of infanticidal males.

However, what Darwin did not explain by his theory was why choosy females and competing males seemed more common than choosy males and competing females. Later researchers have tried to explain this phenomenon based on Bateman's classical experiment on fruit flies. After allowing a small number of fruit flies, *Drosophila melanogaster*, with visible genetic markers to mate and reproduce for a couple of days, Bateman was able to count the offspring sired by different males and females. He thus showed that males had higher variance in reproductive success than females and this result was taken as evidence of male-male competition and female choice, thus sexual selection in action. This experiment has led many to believe that sexual selection is always stronger in males. Hence within-sex reproductive competition between females has been considered

less important than sexual selection in males, and sexual selection in females has received less attention. Later theoretical work has revealed that Bateman's result could be explained by both sexes mating randomly (e.g. no mate choice or male competition) (see Gowaty and Hubbell, 2005). Thus, differential variance in reproductive success between the sexes cannot alone be inferred as evidence for sexual selection in process.

Furthermore, evidence of strong sexual selection in females is common, for example, marmoset dominant females inhibit subordinates' reproduction through behaviour and hormones. In addition, female strategies are often not as obvious as males', but sexual selection is not less important for them, as exemplified by the Hanuman langur females obscuring paternity through multiple mating.

Later researchers extended Bateman's conclusion to explain why females have evolved to be choosy and males indiscriminate based on anisogamy and parental investment. The anisogamy argument states that during the development of recombining gametes (eggs and sperm), selection favoured the evolution of small, mobile gametes (sperm) and large, less mobile gametes (eggs). As a consequence the large gametes became limiting resources for the small gametes, resulting in competition between them. According to this argument, then, male reproductive success is a result of male gametes' access to female gametes. Females, in turn, are limited by their access to biotic and abiotic resources. Parental investment theory suggests that the sex investing most in parenting will be limiting for the other sex. Thus, parental investment theory proposes that the relatively higher costs of reproduction for females favour genes for choosiness in females and indiscrimination and competitiveness in males. These arguments suffer from two problems, first females and males have been subject to much selection after the evolution of different-sized gametes, thus carriers of small, mobile gametes are not necessarily limited by access to females. Second, drawing parallels between the primary selection pressures on male gametes and those affecting male-male contests conceals the importance of selection on interactions between the sexes.

Similarly, our theory concerning mating systems suggests that it is the sex that is most abundantly available to mate that will be sexually selected. Mating system theory is built on the assumption that female reproduction is limited by resources that males monopolize to get access to females. This focus on male behavioural contests for the outcome of mating systems has led to more attention on male rather than female behaviours or interactions between the sexes. Seeing females as resources for males has affected the majority of research on mating systems, though in fact mating systems are a result of the dynamics in the interactions between females and males. Much of evolutionary biology is based on the assumption that mating systems are a function of male competition for resources and thus opportunities to monopolize females, but there are alternative models.

Studying sex-role reversed species as a way to test parental investment theory has resulted in mixed answers. In pipefish and seahorses, the male broods the eggs in a pouch or attached to the stomach and females are therefore predicted to compete among each other for the access to males. In straight-nosed pipefish, *Nerophis ophidion*, females are indeed competing with each other for males and males are choosy. In contrast, seahorse males compete for females despite their large investment in parental care, and both males and females perform mate choice. Seahorse males are thus not limiting female reproductive success. Hence, for many sex-role reversed species, it is still unclear how ecological conditions favour asymmetries in behaviours of the sexes.

In contrast to the aforementioned models of genes for innate choosiness in females and indiscrimination in males, Patricia Gowaty has suggested that selection favours individuals that are flexible and dynamic in their mating behaviour. This hypothesis has generated a model of gender-neutral flexible sex roles³ (see below).

Still another way in which female behaviours have been neglected in sexual selection theory is that differential reproduction can actually result from other interactions besides mate choice. For example, male fruit flies transfer proteins to females during mating that induce females to prolong their inter-mating periods. Thus, males can manipulate females into being less willing to mate and females' choosiness need not be inherent.

An additional critique towards the theory of sexual selection has been the focus on a two-sex system – the males and females as general model does not apply to the diversity of genders in nature. There are hermaphroditic species, species with up to 500 different sexes and species with alternative reproductive strategies.

In conclusion, sexual selection theory has a long history of androcentric bias in both theory and practice. However, this field of study is changing.

SEXUAL SELECTION THEORY AND RESEARCH AT PRESENT

The consciousness of both men and women to feminist issues has increased in evolutionary biology. To date, the 'normal science' of sexual selection has come to incorporate a wide array of issues, such as female–female competition and male coercion of female choice, not included in Darwin's first presentation of sexual selection theory. Another example is the expanding field of study of 'sexual conflict', in which evolutionary adaptations in both males and females are investigated.

Feminist theory incorporated in evolutionary biology has led to an exploration of hypotheses of male coercion of female mate choice. Large male body size is traditionally explained by male–male competition, but

an alternative suggestion is that males by force coerce female mate choice, as exemplified by coho salmon. According to the traditional view, large males are perceived as preferred by females and small males are usually termed 'sneakers', which are thought to interfere in the females' choice of males. However, surprisingly, it is the males with highest viability and fastest growth rates in juvenile stage that become sneakers. In a recent study, it has also been shown that female coho salmon prefer mating with small males, which leaves them more time for mending their nests and they also lay eggs for a longer time when small males are present (Watters, 2005). Larger males act more aggressively towards females. These findings suggest that large males can instead be labelled 'coercers' and small males 'cooperators' (Watters, 2005).

Currently, as results from, for example, paternity analyses are accumulating evidence for almost ubiquitous female multiple mating, sexual selection theory is transforming. Traditional sexual selection theory may even be replaced by models that better fit contemporary empirical evidence. Roughgarden (2004) points out that evolutionary theory is based on individual competition and that cooperation between animals is neglected. She argues for a refusal of the theory of sexual selection and presents an alternative based on cooperation (Roughgarden, 2004). The latest contribution to the new sexual selection theory is a model by Gowaty and Hubbell (2005). The model is gender neutral (no traits are assigned to males or females beforehand) and examines the evolution of flexible sex roles, i.e. choosy, competitive and indiscriminate behaviour in males and females. Assumptions are based on availability of mates, survival probabilities, life history variables, time constraints due to handling mates and those between matings due to parental care. Future testing of the model will prove whether it is better at predicting sex roles than sexual selection theory.

Though sexual selection theory has come far from the Victorian ideas that once influenced it, there still remains gender bias in the eye of the beholder, as has been shown in an illuminating article by Lawton et al. (1997). In an analysis of ornithological natural history narratives, Lawton et al. (1997) reveal gender bias in descriptions of behaviour at the level of molecular analysis as well as the individual and population level. One striking example is when Pinyon jay researchers ignored the importance of female aggression and depicted it as a bird version of PMS called pre-breeding syndrome, while in the light of Lawton et al.'s (1997) analysis, females were simply contesting for breeding territories.

At the same time as evolutionary theory and research on animals are becoming less gender biased, a new branch of sociobiology is flourishing, namely evolutionary psychology. Evolutionary psychology provides evolutionary explanations of human behaviour and considers the parental investment hypothesis an axiom. Current changes in the comprehension of sex roles and sex differences of evolutionary biology are thus not incorporated

in evolutionary psychology, which is also extensively criticized by biologists (e.g. Fausto-Sterling et al., 1997; Gowaty, 2003), not to mention by feminists and social scientists. Vandermassen (2004) urged feminists to incorporate findings of evolutionary psychology into feminist theory. On the contrary, following the arguments put forward earlier, I caution against such an unre-served assimilation.

In conclusion, due to evolutionary psychology's outdated view of sexual selection, I advise against its inclusion in feminist theory. Instead, I suggest that evolutionary theory and research have much to gain from the ongoing integration of gender perspectives. Sexual selection theory has a history burdened by androcentric bias, which is mirrored in contemporary research. Presuppositions of male and female behaviour still shadow our perception of the diversity that nature entails. A patriarchal gender order still characterizes science and the academia (Harding, 2005). We need to increase the awareness of gendering in evolutionary research in order to develop an evolutionary biology that is characterized by gender-neutral notions in both theory and practice.

NOTES

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1. Space restrictions do not permit referencing all original articles. Interested readers are welcome to contact the author for an expanded reference list.
2. This overview is largely influenced by Gowaty (1997, 2003), Gowaty and Hubbell (2005), Zuk (2002), Roughgarden (2004), Fausto-Sterling et al. (1997) and Hrdy (1981).
3. The current definition of conventional sex roles (indeed, an anthropomorphic term) in biology is based on traditional sexual selection theory and thus defined as males competing for female mating partners and females performing mate choice.

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